

### 3.—Two species of the extinct genus *Sthenurus* Owen (Marsupialia, Macropodidae) from south-eastern Australia, including *Sthenurus gilli* sp. nov.

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A new species of *Sthenurus*, smaller than any so far known, is described from deposits near Strathdownie, Western Victoria, of presumed Pleistocene age. A variant of the same species occurs in Haystack Cave, Naracoorte, South Australia, and it may have ranged into Western Australia.

A second (larger) species of *Sthenurus*, resembling *S. occidentalis* Glauert, occurs in the Strathdownie deposit. The Haystack Cave deposit also contains a second species of *Sthenurus* resembling *S. occidentalis*. The taxonomic relationships of the larger Strathdownie species, the larger Haystack Cave species, *S. occidentalis* and *S. oreas* are to be considered later in a separate paper.

#### Introduction

During an investigation of occurrences of the genus *Sthenurus* in Western Australia, I was able to borrow an extensive series of specimens

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from the National Museum of Victoria, for comparative purposes. Among them was a large sample from a site near Strathdownie in western Victoria, representing two species. One of these resembled the Mammoth Cave sample from which Glauert (1910 a and b) described *S. occidentalis*; the other did not fit any published description. Data on these two species from Strathdownie were assembled, and conclusions from these data are reproduced below.

Another series of specimens loaned by the South Australian Museum included a large sample of *Sthenurus* from Haystack Cave, Naracoorte, South Australia. Two species were present in this sample, probably the same two species as at Strathdownie. Data on the two species from Haystack Cave are also presented below.

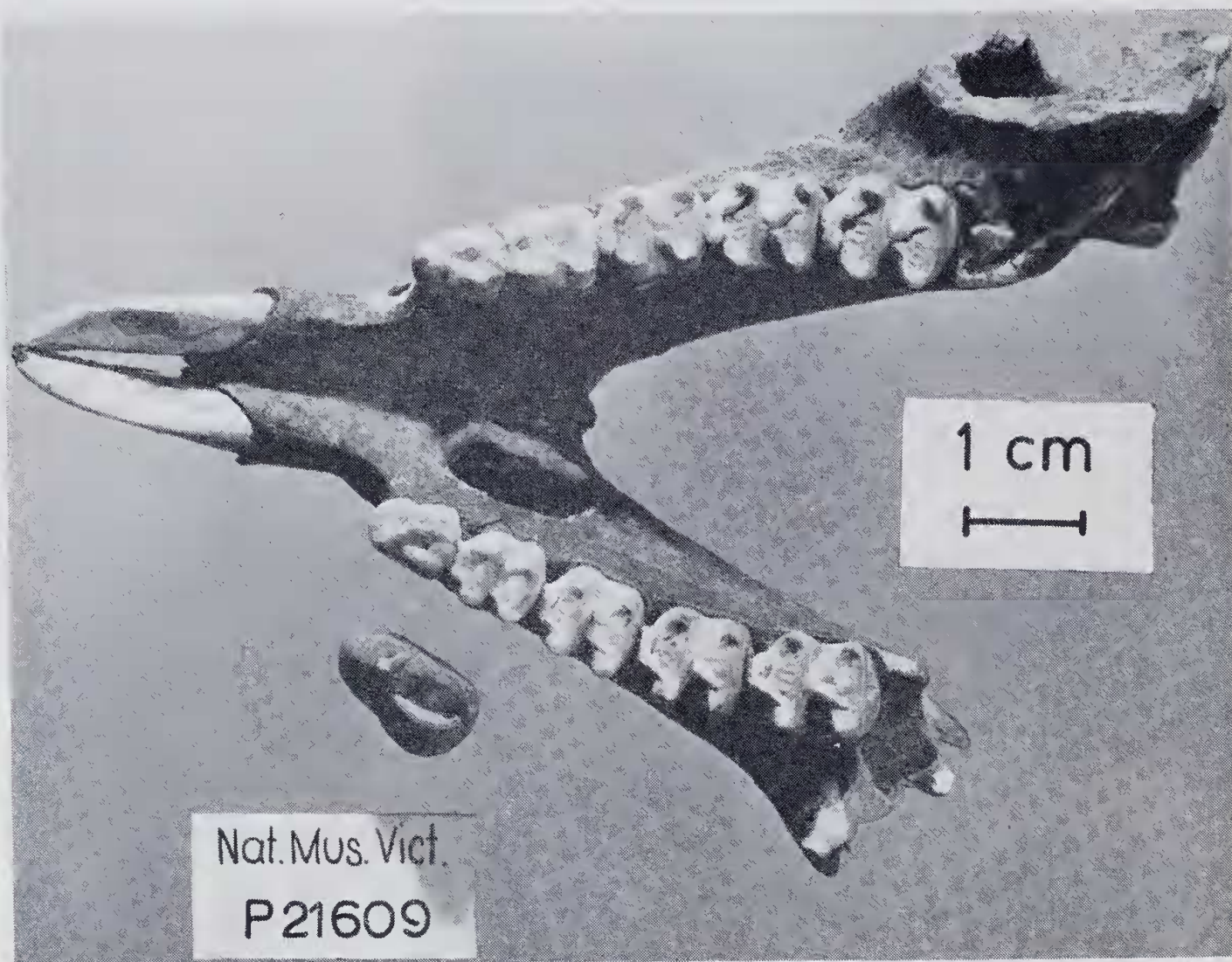
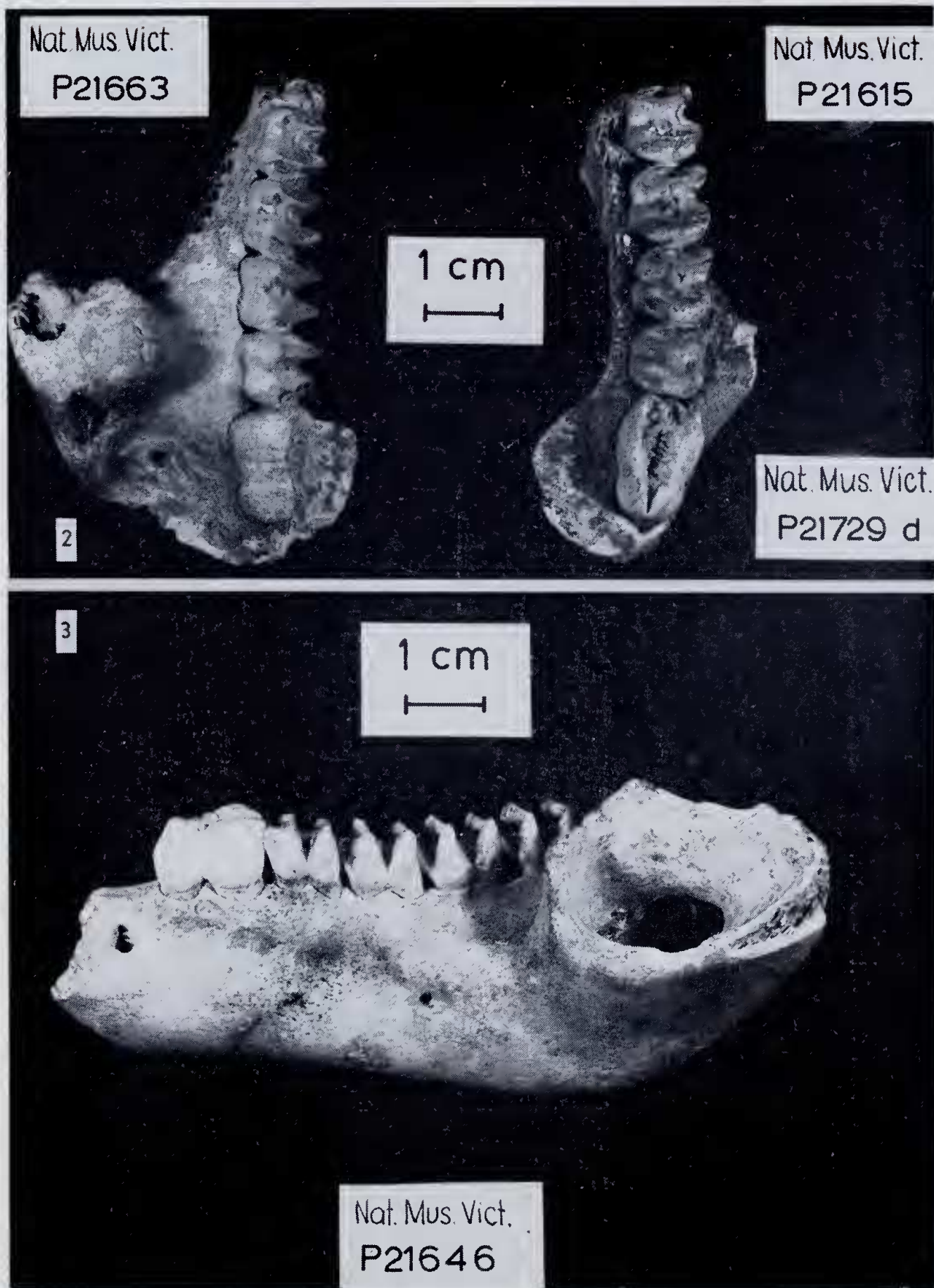


Fig. 1.—*Sthenurus gilli* sp. nov. from Strathdownie, Victoria. Holotype, mandible with left P<sub>4</sub> excavated.



Figs. 2, 3.—*Sthenurus gilli* sp. nov. from Strathdownie, Victoria. 2.—Upper cheek teeth in different aspects, P 21729 d (P<sup>+</sup>) originally separate from P 21615 (molars in maxilla). Note subdued masseteric process, undamaged in P 21663. 3.—Left mandibular ramus, buccal aspect.

Copies of the raw data have been lodged in the libraries of the National Museum of Victoria (Russell St., Melbourne C.1., Victoria), of the South Australian Museum (North Terrace, Adelaide, S.A.) and of the Western Australian Museum (Beaufort St., Perth, Western Australia).

### The Strathdownie Deposit

Gill (1957) describes the Strathdownie deposit as containing a rich and varied assemblage of marsupials, with one monotreme. He states that it occurs in a limestone ridge standing some 20 ft. above the level of a plain extending from Casterton to Mt. Gambier, one of a series of such limestone ridges. The limestone is described as a beach or shallow water sediment containing marine molluscs. It is believed to have been subjected to cave formation during the latter part of the Pleistocene, and the fossil remains were found in red "cave earths" revealed by quarrying.

The specimens described below were presented to the National Museum of Victoria in 1956 and 1957 by Messrs. C. Austin, W. Brooker and C. B. Sasse.

### The *Sthenurus* sample from Strathdownie

This consists of 186 specimens in an excellent state of preservation, from isolated teeth to maxillae and mandibular rami bearing complete sets of teeth. 65 of these specimens show teeth generally rather larger than those of *Sthenurus occidentalis* from Mammoth Cave, and 121 show teeth conspicuously smaller. It is concluded below that the two groups within the Strathdownie sample represent two species of *Sthenurus*. At least 9 individuals of the larger species are represented, and at least 23 of the smaller.

For statistical purposes, care has been taken that each individual animal has been represented only once for each dimension. For example, when considering the dimension "length" of lower permanent premolar, specimens from the left-hand side were first assembled. Each right-hand lower permanent premolar was then compared with each left-hand permanent premolar in general form and in state and pattern of wear. Any right premolar which could be construed as coming from the opposite side of the same animal as any of the left premolars was then rejected from the statistical treatment, and only those right premolars judged to derive from additional animals were accepted. Tables 1 and 2 record distribution of specimens between right and left sides, and the tables of raw data to be lodged in the libraries of the Western Australian Museum and the National Museum of Victoria record the side from which each specimen measured derives. I have examined 7 skulls or ankylosed mandibles of *Sthenurus* showing the cheek teeth of both sides, in none of which was there any sign of differential form or wear between the two sides.

Thus Tables 1 and 2 record maximum numbers of individuals for each dimension, but without the bias which might result from the double representation of some individuals and single representation of others if every available specimen had been included.

For ease of comparison, data have been tabulated in the same form as Marcus (1962) used for his *Sthenurus andersoni* from Bingara, N.S.W. Dental anatomical terms are as used by Ride (1961); tooth designations are those of Thomas, used for the reasons advocated by him (Thomas, 1922) and by Ride (1964). Methods of measurement are detailed with the records of raw data mentioned above.

### *Sthenurus* Owen

A diagnosis of the genus *Sthenurus*, with some comments, has been published recently by Bartholomai (1963). It should be noted that the premolar designation used by Bartholomai differs from that of Thomas (1922) used herein.

### *Sthenurus gilli*\* sp. nov.

**Diagnosis.**— $M_2$ ,  $3$ ,  $4$  narrower than any known species of *Sthenurus* (i.e. than *S. atlas* Owen, *S. andersoni* Marcus, *S. pales* (De Vis) *S. notabilis* Bartholomai, *S. antiquus*, Bartholomai, *S. creas* (De Vis) or *S. occidentalis* Glauert). Lower molars with trigonid basin having an inclined facet to the forward face with several (usually 3) small depressions or furrows in it. Upper molars with wide anterior shelf divided by longitudinal ridglet into larger buccal and smaller lingual portions.

**Holotype.**—National Museum of Victoria specimen P21609, ankylosed right and left mandibular rami, both lacking coronoid and condylar regions. Full juvenile dentition preserved, except hindmost molar on left. Left permanent premolar excavated, showing crown fully formed, and portion of roots. See Fig. 1.

**Type locality.**—Shire Quarry, Section 22, Parish of Kaladbro, Strathdownie, western Victoria.

**Paratypes.**—Same locality as holotype.

(a) Used in statistics, Table 1:—

Nat. Mus. Vict. specimens P21587, 21598, 21607-21609, 21613, 21614, 21618, 21621, 21624, 21642, 21643, 21645-21648, 21654, 21655, 21657, 21659, 21662, 21666, 21677, 21681, 21724c, 21729c, 21732p (mandibular) and P21611, 21615-21617, 21626, 21635, 21637, 21649, 21671, 21674, 21683, 21701, 21724h, 21724i, 21725c, 21729d (maxillary).

(b) Not used in statistics:—

Nat. Mus. Vict. specimens P21595, 21597, 21612, 21619, 21630, 21636, 21652, 21688, 21704, 21706, 21732c, 21732e-g, 21732i-n (mandibular) and P21627, 21634, 21650, 21653, 21663, 21676, 21703, 21724a, 21724d, 21724f, 21725d, 21728a, 21729a (maxillary).

Some isolated molar teeth, both upper and lower, were not included in the statistics because their position in the tooth-row was not certain.

(c) Premaxillary specimens, believed to be referable to *S. gilli*, but not certainly associated with any maxillary specimen:—

Nat. Mus. Vict. specimens P21700, 21730b, 21730d, 21730f, 21730h-i, 21731, 21732r-s, 21733a, 21733c-d.

\*Named after E. D. Gill, Curator of Fossils, National Museum of Victoria, in recognition of his stimulating contributions to our understanding of Australian Quaternary events.

**Table 1**  
*Dental Data on Sthenurus gilli from Strathdownie, Victoria.*

| Dimension Examined* |        | Number of Specimens | Observed Range |  | Sample Mean | Sample Standard Deviation | Sample Coefficient of Variation |
|---------------------|--------|---------------------|----------------|--|-------------|---------------------------|---------------------------------|
|                     |        |                     | Right Side     |  |             |                           |                                 |
| P <sup>3</sup>      | Length | 5                   | 9.4-10.0       |  | 9.82        | 0.25                      | 2.5                             |
|                     | Width  | 5                   | 8.2-9.9        |  | 9.12        | 0.61                      | 6.6                             |
| DP <sup>1</sup>     | Length | 5                   | 8.6-8.9        |  | 8.80        | 0.12                      | 1.4                             |
|                     | Width  | 5                   | 8.9-9.7        |  | 9.26        | 0.28                      | 3.0                             |
| P <sup>1</sup>      | Length | 12                  | 15.2-18.3      |  | 15.98       | 0.92                      | 5.7                             |
|                     | Width  | 12                  | 9.9-12.5       |  | 10.95       | 0.87                      | 8.0                             |
| M <sup>1</sup>      | Length | 10                  | 9.3-10.3       |  | 9.79        | 0.30                      | 3.1                             |
|                     | Width  | 11                  | 9.1-10.2       |  | 9.67        | 0.36                      | 3.7                             |
| M <sup>2</sup>      | Length | 8                   | 10.0-10.9      |  | 10.41       | 0.37                      | 3.6                             |
|                     | Width  | 8                   | 9.4-10.6       |  | 9.95        | 0.51                      | 5.1                             |
| M <sup>3</sup>      | Length | 5                   | 10.3-12.0      |  | 11.18       | 0.62                      | 5.5                             |
|                     | Width  | 5                   | 9.7-10.8       |  | 10.00       | 0.45                      | 4.5                             |
| M <sup>4</sup>      | Length | 2                   | 9.9-10.7       |  | 10.30       | 0.57                      | 5.5                             |
|                     | Width  | 2                   | 9.4-9.5        |  | 9.45        | 0.07                      | 0.7                             |

| Dimension Examined* |             | Holotype Nat. Mus. Vict. P 21609 (Right Side) | Number of Specimens |       | Observed Range | Sample Mean | Sample Standard Deviation | Sample Coefficient of Variation |
|---------------------|-------------|-----------------------------------------------|---------------------|-------|----------------|-------------|---------------------------|---------------------------------|
|                     |             |                                               | Left                | Right |                |             |                           |                                 |
| I <sub>1</sub>      | Depth       | 9.5                                           | 6                   | 0     | 9.4-10.2       | 9.73        | 0.70                      | 7.2                             |
| P <sub>3</sub>      | Length      | 8.1                                           | 5                   | 7     | 8.1-8.9        | 8.73        | 0.25                      | 2.8                             |
|                     | Width       | 6.5                                           | 5                   | 7     | 6.5-8.1        | 7.34        | 0.40                      | 5.4                             |
| DP <sub>1</sub>     | Length      | 7.8                                           | 5                   | 7     | 7.6-8.4        | 7.97        | 0.26                      | 3.2                             |
|                     | Width       | 7.3                                           | 5                   | 7     | 7.3-7.9        | 7.48        | 0.20                      | 2.7                             |
| P <sub>4</sub>      | Length      | 13.3                                          | 9                   | 7     | 13.3-15.0      | 14.36       | 0.49                      | 3.4                             |
|                     | Width       | 8.2                                           | 9                   | 6     | 8.0-9.3        | 8.60        | 0.41                      | 4.8                             |
|                     | Basin Width | 3.8                                           | 6                   | 8     | 3.8-5.5        | 4.45        | 0.41                      | 9.2                             |
| M <sub>1</sub>      | Length      | 8.5                                           | 9                   | 6     | 8.4-9.3        | 8.81        | 0.28                      | 3.2                             |
|                     | Width       | 8.0                                           | 9                   | 6     | 7.8-8.2        | 8.01        | 0.12                      | 1.5                             |
| M <sub>2</sub>      | Length      | 9.6                                           | 8                   | 4     | 9.5-9.9        | 9.67        | 0.13                      | 1.3                             |
|                     | Width       | 8.3                                           | 8                   | 4     | 8.2-8.8        | 8.53        | 0.20                      | 2.4                             |
| M <sub>3</sub>      | Length      | 9.7                                           | 4                   | 4     | 9.7-10.7       | 10.13       | 0.36                      | 3.6                             |
|                     | Width       | 8.8                                           | 4                   | 4     | 8.8-9.9        | 9.19        | 0.33                      | 3.6                             |
| M <sub>4</sub>      | Length      |                                               | 2                   | 2     | 9.5-9.9        | 9.70        | 0.18                      | 1.9                             |
|                     | Width       | in alveolus                                   | 2                   | 2     | 9.1-9.5        | 9.33        | 0.17                      | 1.9                             |

\* Details of measuring procedures, with estimates of accuracy and consistency, lodged with data on individual specimens in National Museum of Victoria and Western Australian Museum. All dimensions maximal, widths in molars across protoloph or protolophid, depth I<sub>1</sub> perpendicular to long axis of tooth, basin width P<sub>4</sub> across posterior central basin.

**Comparison of *S. gilli* with other species**

See Figs. 1 (holotype, showing lower dentition), 2 (upper dentition) and 3 (buccal aspect of mandibular ramus), and Table 1.

Distinguishable from *S. andersoni* Marcus by procumbency of lower incisor (much less procumbent in *S. gilli*) and by width of P<sub>3</sub>, P<sub>4</sub> and M<sub>2-4</sub>; in *S. gilli*, P<sub>3</sub> and P<sub>4</sub> wider but M<sub>2,3,4</sub> narrower than in *S. andersoni*. Trigonid basin projecting relatively further forward, and cheek tooth row (P<sub>3</sub>, DP<sub>1</sub>, M<sub>1-1</sub> inclusive in juveniles) much longer, in *S. andersoni* than in *S. gilli*. Upper permanent premolars not known in *S. andersoni*, but upper molars stated by Marcus (1962) to lack forelink.

Distinguishable from *S. occidentalis* Glauert and from the larger Strathdownie species not only by dental dimensions, but also by lack of

a prominent descending masseteric (zygomatic) process, and by lack of molar ornamentation. In *S. occidentalis* and in the larger species at Strathdownie, the descending process is very marked, projecting downward further than the occlusal surface of the upper cheek tooth row, whereas in *S. gilli* it is so subdued and smoothly rounded as hardly to justify the term "process." In *S. occidentalis* and in the larger Strathdownie species, there is much more ornamentation on both upper and lower molars than in *S. gilli*.

I have been able to make direct comparison of *S. gilli* specimens with only one specimen of *S. oreas* (De Vis), viz. Queensland Museum specimen F3814, figured by Bartholomai (1963—Fig. 5). This specimen, portion of a maxilla, differs markedly from any specimen of *S. gilli*

not only in the greater lengths and widths of molars in *S. oreas*, but also in their showing much more ornamentation.

From Bartholomai's (1963) description of his revised *S. oreas*, it would appear that the mandibular ramus in *S. oreas* closely resembles that of *S. gilli* in form, except that the masseteric crest and masseteric foramen would appear to be a little lower in *S. gilli* (see Fig. 3); however, in almost all quantitative respects (except width of lower permanent premolar), both bone and teeth appear to be markedly smaller in mandibles of *S. gilli* than *S. oreas*.

The small size of the molar teeth in *S. gilli* suffices to distinguish this species from any other species of *Sthenurus*. However, two aspects of tooth morphology also appear to be distinctive of *S. gilli*, those noted in the diagnosis above, one for upper and one for lower molars.

#### The larger species of *Sthenurus* at Strathdownie

##### Specimens.—

(a) Used in statistics, Table 2.—

Nat. Mus. Vict. specimens P21586, 21633, 21638, 21640, 21644, 21656, 21724a, 21724b, 21725b, 21729b, 21732a-b, 21732d (mandibular) and P21629, 21641, 21660, 21673, 21687, 21705, 21720b, 21724g, 21725a, 21728c, 21729e (maxillary).

(b) Not used in statistics:—

Nat. Mus. Vict. specimens P21732o (mandibular), P21672, 21721h, 21728b, 21749 (maxillary) and P21678, 21730g, 21733b, 21733e (premaxillary).

Some isolated lower molars were not included in the statistics because their position in the tooth row was not certain.

#### Comparison of larger Strathdownie species with other species

See Figs. 4 (showing upper dentition) and 5 (showing lower dentition) and Table 2 (of dental dimensions).

Closely resembles *S. occidentalis* Glauert and *S. oreas* (De Vis) in form. In lengths  $P_3^3$  and widths  $M_{1,4}^{1,4}$  considerably exceeds Mammoth Cave sample of *S. occidentalis* (direct comparison—D.M.). In lengths  $P_4^4$  and widths  $M_{1,2}^{1,3}$  exceeds Queensland sample of *S. oreas*, according to data published by Bartholomai (1963) and to my direct comparison with one Queensland specimen (F3814—see above). Despite the quantitative differences observed between the large Strathdownie sample and those from Mammoth Cave and from Queensland, I believe the animals concerned were related, and propose to investigate the relationship further. In the meantime, it appears desirable to leave open the matter of the taxonomic status of the larger *Sthenurus* at Strathdownie.

Distinguishable from *S. antiquus* Bartholomai on the form of the lower permanent premolar and the spacing of the lower molars, according to my direct comparison with Queensland Museum specimens F2931 and F2932, figured in association by Bartholomai (1963—Fig. 9). In the larger Strathdownie specimens, each lower

molar overlaps the base of the preceding tooth in the cheek tooth row to a greater extent than in *S. antiquus*. The lingual crest on the lower permanent premolar F2932 of *S. antiquus* inclines inward to a much greater extent, and the buccal crest is relatively much lower, extends less far forward, and is more clearly separated on the rear face of the tooth from the lingual crest, than in any  $P_4$  from the larger Strathdownie species.

#### Upper incisors of *Sthenurus* at Strathdownie

No specimens were available in the Strathdownie sample which associated upper molars or premolars referable to *S. gilli* with upper incisors. However, available  $I^1$  and  $I^2$  specimens from Strathdownie fell into two distinct groups, larger and smaller; it would appear justifiable to associate the smaller incisors with *S. gilli* rather than with the larger species occurring at Strathdownie. Unfortunately, no specimen showed an  $I^3$  associated with a smaller  $I^2$  or  $I^1$ ; but it was possible to divide the  $I^3$  specimens available into two kinds. One of these groups could be associated with  $I^2$  and  $I^1$ , and clearly derived from the larger species at Strathdownie; furthermore, in form this group resembled the  $I^3$  teeth of *S. occidentalis*. In the second of the  $I^3$  groups, the individual teeth were more strap-like than  $I^3$  in *S. occidentalis*, but were less rugose on the lingual aspect, and bore a less pronounced "fold" in the enamel of the lingual aspect of the antero-occlusal corner of the tooth. Since the larger Strathdownie species resembled *S. occidentalis* in many particulars, it would appear reasonable to assign the more strap-like upper third incisors to *S. gilli* rather than to the larger species.

It is on these grounds that the allotment of incisor teeth to the two different species in the Strathdownie deposit has been made. See Fig. 5.

S. Aust. Mus. specimen P 13687, attributable to *Sthenurus gilli* (see below) does show  $I^1$  and  $I^3$ , but unfortunately not  $I^2$ , in association with cheek teeth distinctive of this species. See Fig. 7. It confirms the division made among the unattached Strathdownie upper incisors.

#### The Haystall Cave Deposit

According to labels supplied with the specimens from Haystall Cave, all the specimens on loan to me appear to have been recovered from a red to yellow sandy deposit at depths up to 2 ft. 6 in. One left mandibular ramus (P 13682) from the top 6 in. appears to derive from the same animal as right ramus P 13830a from 2 ft. 6 in.; thus it is probable that all the specimens are approximately contemporaneous. They are probably of late Quaternary age.

The sample was collected and presented to the South Australian Museum in 1963 and 1964 by the Cave Exploration Group (South Australia).

#### The *Sthenurus* sample from Haystall Cave

This consists of 52 well-preserved specimens, most of them juveniles, 24 forming a homogeneous group with larger teeth; and 28 forming a similarly homogeneous group with smaller

**Table 2**  
*Dental data on the larger species of Sthenurus from Strathdownie, Victoria.*  
 Upper

| Dimension       | Examined* | Number of Specimens |       | Observed Range | Sample Mean | Sample Standard Deviation | Sample Coefficient of Variation |
|-----------------|-----------|---------------------|-------|----------------|-------------|---------------------------|---------------------------------|
|                 |           | Left                | Right |                |             |                           |                                 |
| P <sup>3</sup>  | Length    | 2                   | 0     | 12.0-12.0      | 12.00       | mm.                       | ...                             |
|                 | Width     | 2                   | 0     | 10.3-10.6      | 10.45       | 0.20                      | 1.9                             |
| DP <sup>4</sup> | Length    | 2                   | 0     | 10.5-11.5      | 11.00       | 0.71                      | 6.5                             |
|                 | Width     | 2                   | 0     | 11.2-12.3      | 11.75       | 0.77                      | 6.6                             |
| P <sup>4</sup>  | Length    | 2                   | 3     | 17.1-18.8      | 18.22       | 0.65                      | 3.6                             |
|                 | Width     | 2                   | 3     | 12.1-13.9      | 13.06       | 0.75                      | 5.7                             |
| M <sup>1</sup>  | Length    | 2                   | 0     | 12.8-13.2      | 13.00       | 0.28                      | 2.2                             |
|                 | Width     | 2                   | 0     | 12.9-13.1      | 13.00       | 0.14                      | 1.1                             |
| M <sup>2</sup>  | Length    | 3                   | 1     | 13.7-14.6      | 14.18       | 0.32                      | 2.3                             |
|                 | Width     | 2                   | 1     | 13.6-14.3      | 13.83       | 0.38                      | 2.8                             |
| M <sup>3</sup>  | Length    | 3                   | 1     | 14.2-15.5      | 14.73       | 0.60                      | 4.1                             |
|                 | Width     | 1                   | 1     | 13.6-13.8      | 13.70       | 0.14                      | 1.0                             |
| M <sup>4</sup>  | Length    | 1                   | 2     | 13.0-14.6      | 13.63       | 0.85                      | 6.3                             |
|                 | Width     | 1                   | 2     | 12.7-14.2      | 13.33       | 0.84                      | 6.3                             |
| Lower           |           |                     |       |                |             |                           |                                 |
| I <sub>1</sub>  | Depth     | 0                   | 3     | 12.0-13.3      | 12.67       | 0.65                      | 5.1                             |
| P <sub>3</sub>  | Length    | 1                   | 2     | 9.6-10.1       | 9.90        | 0.27                      | 2.7                             |
|                 | Width     | 1                   | 2     | 7.7-8.0        | 7.87        | 0.16                      | 2.0                             |
| DP <sub>4</sub> | Length    | 1                   | 1     | 9.7-10.1       | 9.90        | 0.28                      | 2.9                             |
|                 | Width     | 1                   | 1     | 9.0-9.7        | 9.35        | 0.49                      | 5.2                             |
| P <sub>4</sub>  | Length    | 3                   | 5     | 16.0-17.6      | 16.79       | 0.53                      | 3.2                             |
|                 | Width     | 3                   | 6     | 9.8-10.7       | 10.29       | 0.27                      | 2.6                             |
| M <sub>1</sub>  | Length    | 1                   | 4     | 11.5-12.4      | 11.74       | 0.38                      | 3.2                             |
|                 | Width     | 1                   | 4     | 10.1-11.0      | 10.38       | 0.37                      | 3.5                             |
| M <sub>2</sub>  | Length    | 1                   | 1     | 12.7-12.7      | 12.70       | ...                       | ...                             |
|                 | Width     | 1                   | 1     | 11.4-11.9      | 11.65       | 0.35                      | 3.0                             |
| M <sub>3</sub>  | Length    | 1                   | 1     | 13.2-13.4      | 13.30       | 0.14                      | 1.1                             |
|                 | Width     | 1                   | 1     | 12.0-12.2      | 12.10       | 0.14                      | 1.2                             |
| M <sub>4</sub>  | Length    | 1                   | 0     | ...            | 12.80       | ...                       | ...                             |
|                 | Width     | 1                   | 0     | ...            | 11.50       | ...                       | ...                             |

\* All dimensions maximal, widths in molars across protoloph or protolophid, depth I<sub>1</sub> perpendicular to long axis of tooth.

teeth. At least 12 individuals of the larger species are represented, and at least 9 of the smaller.

From these groups, the specimens listed below were selected for statistical purposes in the same way as from the two groups at Strathdownie:—

(a) Larger species. S. Aust. Mus. specimens P 13703, 13831 g-h (maxillary) and P 13674-13676, 13678, 13680-13681, 13696, 13711, 13713-13714, 13830a, 13831 c-d (mandibular).

(b) Smaller species. S. Aust. Mus. specimens P 13687 (complete upper dentition of both sides except right I<sup>2</sup>, left I<sup>2-3</sup>), P 13690 a-b, 13691-13694 (maxillary) and P 13688, 13702, 13704, 13706, 13708, 13710, 13717, 13830 b, 13831 a-b (mandibular).

Measurements on these specimens are summarized in Tables 3 and 4.

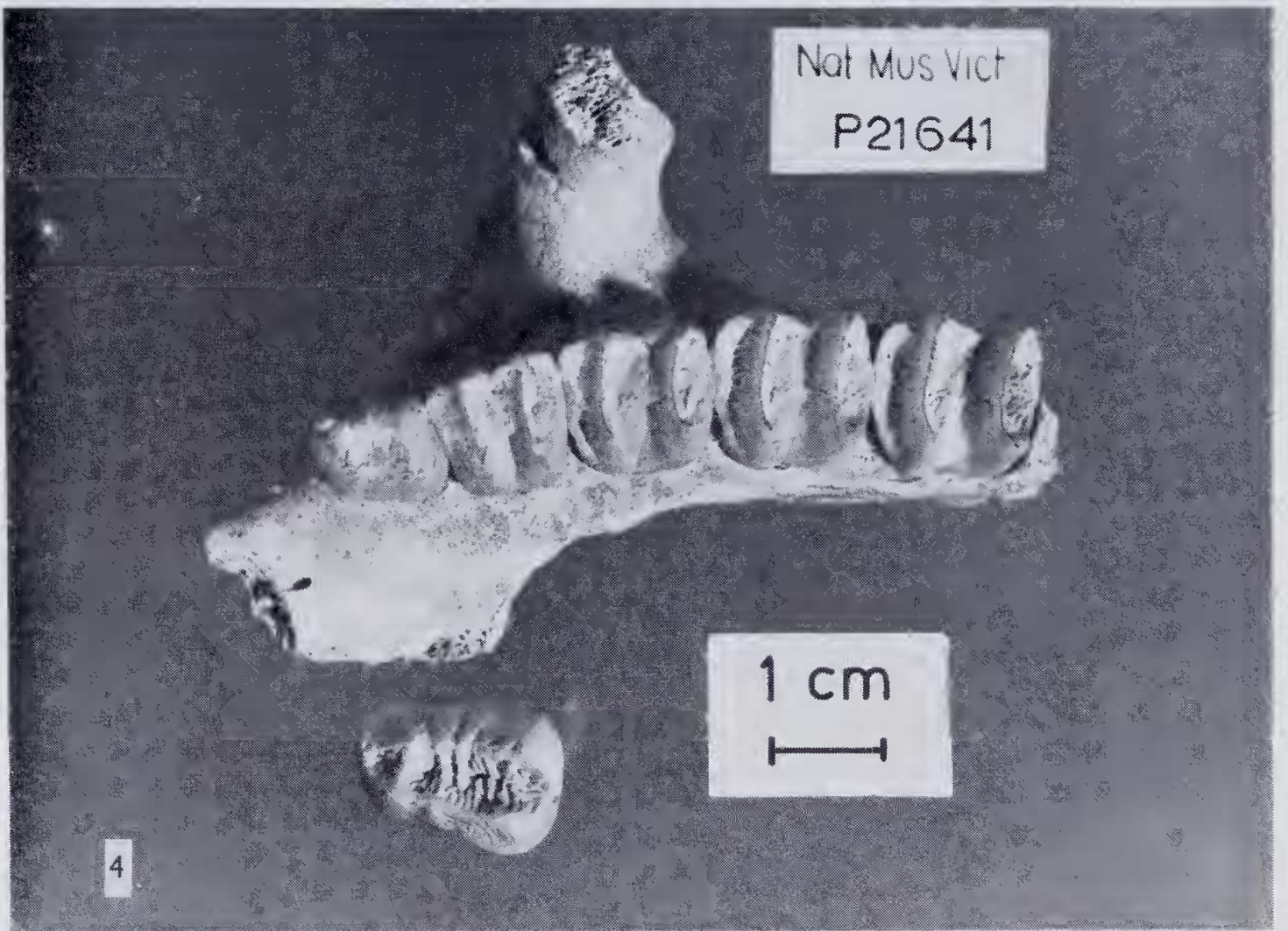
#### The smaller species of *Sthenurus* from Haystack Cave

Direct comparisons of specimens of the smaller Strathdownie with the smaller Haystack Cave species show that the two are closely similar.

On morphological grounds, one would equate them. Compare Figs. 1, 2 and 3 with Fig. 7 below.

However, mean dimensions in the Haystack Cave sample exceed those in the Strathdownie sample in 28 cases out of 30, and there are even 2 cases (length DP<sup>4</sup> and width M<sup>4</sup>) in which ranges in the two samples do not overlap. See Tables 1 and 3.

Such a situation, in which strong morphological resemblances between two samples are coupled with quantitative distinctions, has been discussed by Ride (1964). He has proposed numerical tests for the recognition of subspecies in this situation. On Ride's tests, either length of DP<sup>4</sup> or width of M<sup>4</sup> could conceivably serve to differentiate as subspecies the Haystack Cave and Strathdownie samples of the smaller *Sthenurus*. But none of the differences revealed by comparison of Tables 1 and 3 below can, in my opinion, be construed as differentiating full species. The Haystack Cave sample appears to me to be merely a geographical or temporal variant of *Sthenurus gilli* as defined above.



Figs. 4, 5.—*Sthenurus* sp., the larger species from Strathdownie, Victoria. 4.—Upper cheek teeth, P<sub>4</sub> excavated. Note prominent masseteric process. 5.—Lower cheek teeth, P<sub>4</sub> excavated.

**The larger species of *Sthenurus* from  
Haystack Cave**

Like the smaller species, the larger species at Haystack Cave and at Strathdownie are closely similar in form, but show quantitative differences. Compare Figs. 4 and 5 with Fig. 8, and Table 2 with Table 4. Note that the Haystack Cave sample of lower teeth is the more numerous of the two. In a substantial minority of cases (13 out of 29) mean dimensions (or single measurements where only one specimen occurs) in the less numerous sample fall outside the observed range in the more numerous sample, and in several cases (e.g. length  $P^1$ , depth  $I_1$ , width  $P_3$ ) there is no overlap in range.

Despite the strong resemblances between the two samples, some doubt therefore remains about the grade of their relationship. Since in any case, the question of relationships of both samples with the Darling Downs (Queensland) sample of *Sthenurus oreas* and with the Mammoth Cave (W.A.) sample of *S. occidentalis* are to be taken up later, the question of conspecificity of the Haystack Cave and Strathdownie samples is not further pursued here. Provisionally, the two samples appear to me to be geographical or temporal variants of one species.

**Possible occurrences of the Strathdownie and  
Haystack Cave species of *Sthenurus* in  
Western Australia**

A small lower permanent premolar ( $P_4$ ) of *Sthenurus* was described and figured by Lundelius (1963) from Madura Cave on the Nullarbor Plain. This specimen is now lodged in the Chicago Natural History Museum, but I have examined a plaster cast of it (W. Aust. Mus. specimen 63.6.1). Its length is 14.2 mm., its width 8.1 mm. and its basin width is 3.5 mm., if measurements made from the cast can be taken as accurate. ("Basin width" is the maximum distance separating buccal from lingual crests on the hinder portion of  $P_4$ ).

The Madura Cave tooth resembles  $P_4$  in both Haystack Cave and Strathdownie samples of *S. gilli* in form, and in length falls within the range shown in both samples. In width it falls within the Strathdownie but not quite within the Haystack Cave ranges, and its basin width is smaller than any in these two samples. Only provisionally, therefore, can it be referred to *S. gilli*.

Since his original discovery at Madura Cave, Lundelius has participated in further excavations there (Lundelius E. L. 1964 pers. comm.)

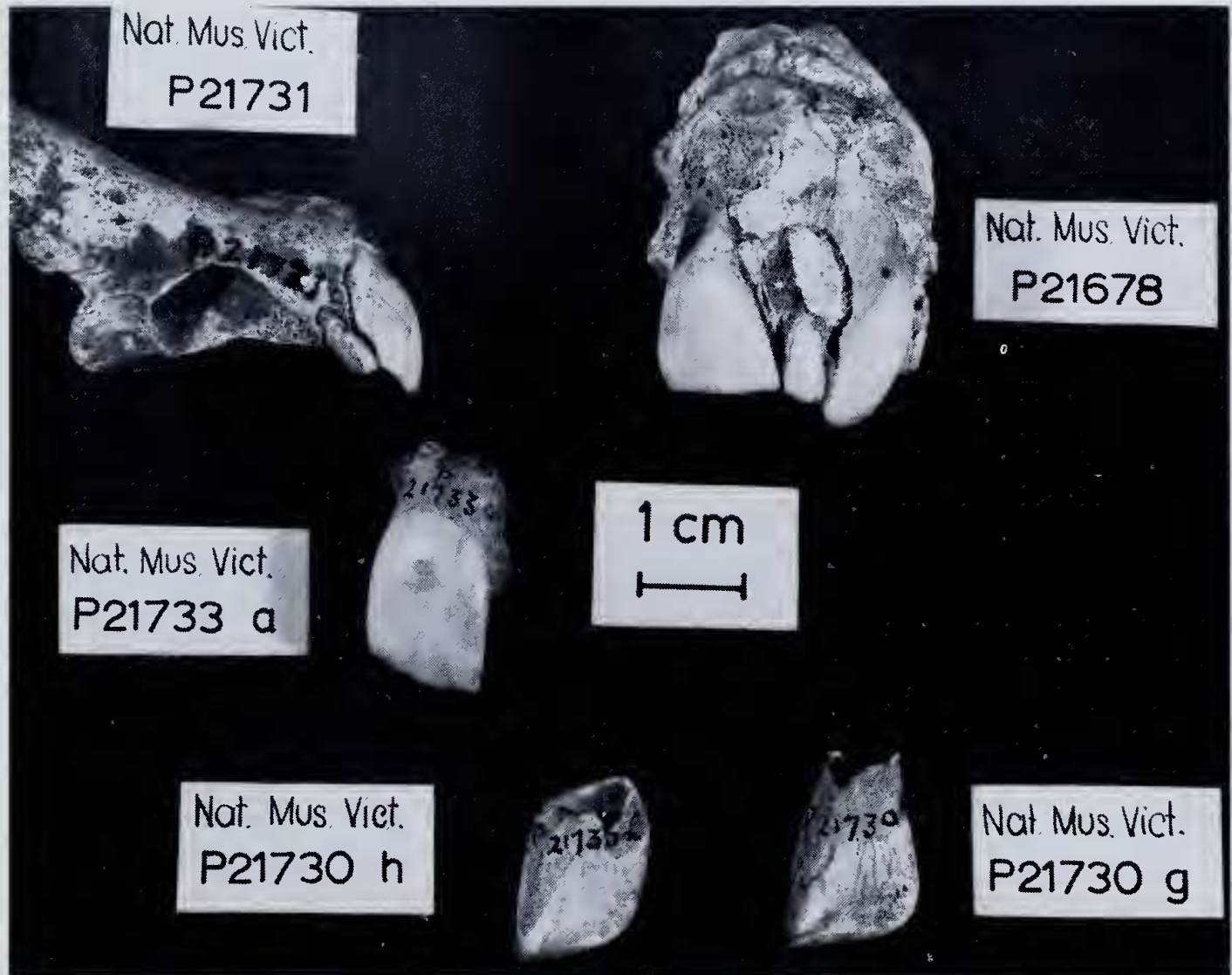


Fig. 6.—Comparison of *Sthenurus* upper incisors from Strathdownie, Victoria. Left, P 21731, P21733 a and P 21730 h attributed to *S. gilli*. Right, P 21678 and P 21730 g attributed to the larger species.



Table 3

Dental data on the smaller species of *Sthenurus* from Haystack Cave, Naracoorte, South Australia.  
Upper

| Dimension Examined*    | Number of Specimens |       | Observed Range | Sample Mean   | Sample Standard Deviation | Sample Coefficient of Variation |
|------------------------|---------------------|-------|----------------|---------------|---------------------------|---------------------------------|
|                        | Left                | Right |                |               |                           |                                 |
| I <sup>1</sup> Length  | 0                   | 1     | mm.<br>.....   | mm.<br>c. 5.9 | mm.<br>.....              | .....                           |
| I <sup>2</sup> Length  | 0                   | 1     | .....          | 12.10         | .....                     | .....                           |
| P <sup>3</sup> Length  | 1                   | 3     | 9.8-10.5       | 10.15         | 0.29                      | 2.8                             |
| P <sup>3</sup> Width   | 1                   | 3     | 8.4-9.3        | 8.90          | 0.37                      | 4.2                             |
| DP <sup>4</sup> Length | 1                   | 3     | 9.3-9.6        | 9.43          | 0.15                      | 1.6                             |
| DP <sup>4</sup> Width  | 1                   | 3     | 9.4-10.2       | 9.80          | 0.34                      | 3.4                             |
| P <sup>4</sup> Length  | 2                   | 4     | 15.2-16.4      | 15.82         | 0.45                      | 2.8                             |
| P <sup>4</sup> Width   | 1                   | 4     | 11.0-12.2      | 11.48         | 0.71                      | 6.2                             |
| M <sup>1</sup> Length  | 0                   | 4     | 10.0-10.6      | 10.23         | 0.27                      | 2.6                             |
| M <sup>1</sup> Width   | 0                   | 4     | 9.9-10.6       | 10.25         | 0.29                      | 2.8                             |
| M <sup>2</sup> Length  | 1                   | 4     | 10.4-11.7      | 10.90         | 0.54                      | 5.0                             |
| M <sup>2</sup> Width   | 1                   | 4     | 10.2-10.9      | 10.56         | 0.25                      | 2.4                             |
| M <sup>3</sup> Length  | 1                   | 2     | 11.3-11.9      | 11.60         | 0.30                      | 2.6                             |
| M <sup>3</sup> Width   | 1                   | 2     | 10.6-11.0      | 10.77         | 0.21                      | 2.0                             |
| M <sup>4</sup> Length  | 1                   | 1     | 10.6-11.0      | 10.80         | 0.28                      | 2.6                             |
| M <sup>4</sup> Width   | 1                   | 1     | 10.1-10.4      | 10.25         | 0.37                      | 3.6                             |

## Lower

|                            |   |   |           |       |      |      |
|----------------------------|---|---|-----------|-------|------|------|
| I <sub>1</sub> Depth       | 0 | 4 | 9.7-11.2  | 10.35 | 0.66 | 6.3  |
| P <sub>2</sub> Length      | 0 | 5 | 8.5-9.4   | 9.10  | 0.39 | 4.3  |
| P <sub>2</sub> Width       | 0 | 5 | 7.1-7.9   | 7.56  | 0.30 | 3.9  |
| DP <sub>1</sub> Length     | 0 | 5 | 8.1-8.6   | 8.26  | 0.19 | 2.3  |
| DP <sub>1</sub> Width      | 0 | 5 | 7.3-8.3   | 7.64  | 0.42 | 5.5  |
| P <sub>1</sub> Length      | 0 | 9 | 13.7-16.2 | 14.97 | 0.78 | 5.2  |
| P <sub>1</sub> Width       | 0 | 9 | 8.3-9.9   | 9.01  | 0.48 | 5.3  |
| P <sub>1</sub> Basin Width | 0 | 7 | 4.1-5.4   | 4.69  | 0.52 | 11.0 |
| M <sub>1</sub> Length      | 0 | 8 | 8.5-9.5   | 9.13  | 0.34 | 3.7  |
| M <sub>1</sub> Width       | 0 | 9 | 7.9-9.0   | 8.37  | 0.41 | 4.9  |
| M <sub>2</sub> Length      | 0 | 6 | 9.3-10.8  | 9.93  | 0.53 | 5.3  |
| M <sub>2</sub> Width       | 0 | 6 | 8.5-9.7   | 8.93  | 0.49 | 5.5  |
| M <sub>3</sub> Length      | 0 | 4 | 9.7-11.1  | 10.35 | 0.58 | 5.6  |
| M <sub>3</sub> Width       | 0 | 4 | 9.1-10.4  | 9.60  | 0.59 | 6.2  |
| M <sub>4</sub> Length      | 0 | 2 | 9.5-10.4  | 9.95  | 0.64 | 6.3  |
| M <sub>4</sub> Width       | 0 | 2 | 9.4-10.4  | 9.90  | 0.71 | 7.1  |

\* All dimensions maximal. widths in molars across protoleph or protolephid. depth I<sub>1</sub> perpendicular to long axis of tooth.

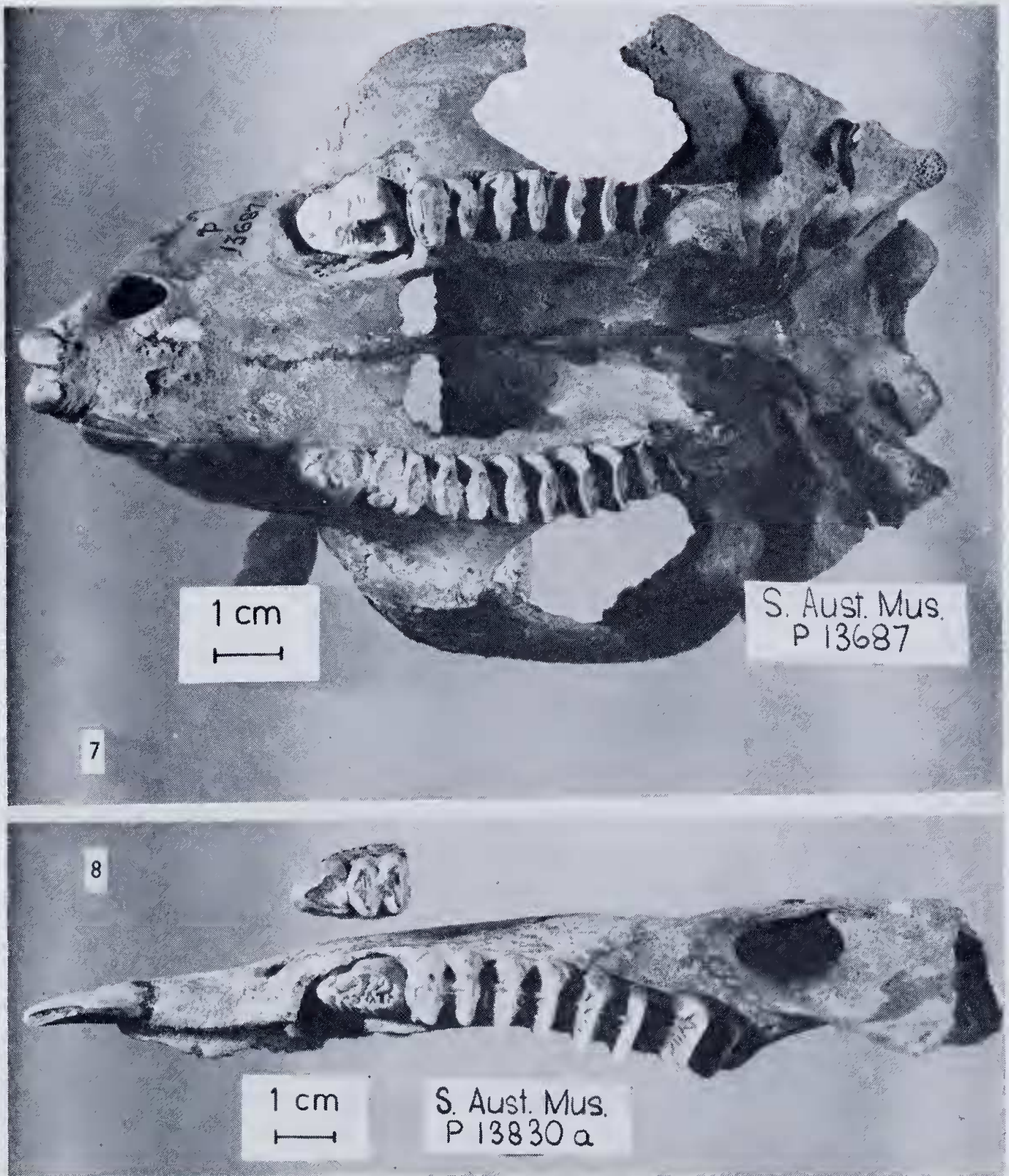
but without finding any more specimens of *Sthenurus*. It is unfortunate that a single premolar does not necessarily provide more than a general guide to the probable size of the molars in *Sthenurus*. For example, *S. oreas* (De Vis) as revised by Bartholomai (1963) has lower permanent premolars which are shorter than those of *S. occidentalis* Glauert, together with lower molars which are longer. Both premolars and molars are similar in form. If, in these samples, only premolars had been known, one might have predicted from them that the molars of *S. oreas* would have been shorter than those of *S. occidentalis*. By analogy, it is possible that the molars of the Madura Cave species of *Sthenurus* may have differed quite markedly from those of *S. gilli*.

Tentatively, however, it may be suggested that *Sthenurus gilli* ranged into Western Australia.

As remarked above, the larger species of *Sthenurus* at Haystack Cave and at Strathdownie resemble *S. occidentalis* from Mammoth Cave, W.A. in form and in size of the lower permanent premolars, but not closely in size of the molars. These samples could conceivably represent geographical variants of a wide-ranging species which once included Western Australia in its range.

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I am indebted to Mr. E. D. Gill (Curator of Fossils, National Museum of Victoria), to Dr. D. W. P. Corbett (Curator of Fossils and



Figs. 7, 8.—*Sthenurus* from Haystack Cave, South Australia. 7.—Variant of *Sthenurus gilli* sp. nov. Skull with left  $P^3$  and  $DP^4$  removed to expose  $P^1$ . 8.—The larger species of *Sthenurus* at Haystack Cave. Right mandibular ramus with  $P^3$  and  $DP^4$  displaced to the side, exposing  $P^1$ .

**Table 4**

*Dental data on the larger species of Sthenurus from Haystack Cave, Naracoorte, South Australia.*

Upper

| Dimension Examined* |        | Number of Specimens |       | Observed Range | Sample Mean | Sample Standard Deviation | Sample Coefficient of Variation |
|---------------------|--------|---------------------|-------|----------------|-------------|---------------------------|---------------------------------|
|                     |        | Left                | Right |                |             |                           |                                 |
| P <sup>3</sup>      | Length | 0                   | 1     | mm.            | mm.         | mm.                       |                                 |
|                     | Width  | 0                   | 1     | ....           | 10.80       | ....                      | ....                            |
| DP <sup>1</sup>     | Length | 0                   | 1     | ....           | 11.00       | ....                      | ....                            |
|                     | Width  | 0                   | 1     | ....           | 10.60       | ....                      | ....                            |
| P <sup>1</sup>      | Length | 0                   | 2     | 16.7-16.8      | 16.75       | 0.10                      | 0.6                             |
|                     | Width  | 0                   | 2     | 12.0-12.5      | 12.25       | 0.35                      | 2.9                             |
| M <sup>1</sup>      | Length | 0                   | 1     | ....           | 12.10       | ....                      | ....                            |
|                     | Width  | 0                   | 1     | ....           | 11.50       | ....                      | ....                            |
| M <sup>2</sup>      | Length | 1                   | 0     | ....           | 14.30       | ....                      | ....                            |
|                     | Width  | 1                   | 0     | ....           | 13.60       | ....                      | ....                            |
| M <sup>3</sup>      | Length | 1                   | 0     | ....           | 14.30       | ....                      | ....                            |
|                     | Width  | 1                   | 0     | ....           | 13.80       | ....                      | ....                            |
| M <sup>4</sup>      | Length | 1                   | 0     | ....           | 13.10       | ....                      | ....                            |
|                     | Width  | 1                   | 0     | ....           | 12.70       | ....                      | ....                            |

Lower

|                 |        |   |   |           |       |      |     |
|-----------------|--------|---|---|-----------|-------|------|-----|
| I <sub>1</sub>  | Depth  | 4 | 1 | 10.9-11.6 | 11.26 | 0.79 | 7.0 |
| P <sub>3</sub>  | Length | 8 | 1 | 9.4-10.4  | 9.90  | 0.42 | 4.2 |
|                 | Width  | 8 | 1 | 8.7-9.7   | 8.98  | 0.38 | 4.2 |
| DP <sub>1</sub> | Length | 8 | 1 | 9.3-10.5  | 10.05 | 0.43 | 4.3 |
|                 | Width  | 8 | 1 | 8.7-9.9   | 9.29  | 0.35 | 3.7 |
| P <sub>4</sub>  | Length | 8 | 3 | 15.5-17.5 | 16.45 | 0.54 | 3.3 |
|                 | Width  | 9 | 2 | 9.1-10.6  | 9.85  | 0.38 | 3.8 |
| M <sub>1</sub>  | Length | 7 | 2 | 11.6-12.3 | 11.90 | 0.57 | 4.8 |
|                 | Width  | 7 | 2 | 9.8-10.9  | 10.32 | 0.32 | 3.5 |
| M <sub>2</sub>  | Length | 1 | 3 | 12.9-14.0 | 13.70 | 0.54 | 3.9 |
|                 | Width  | 1 | 2 | 11.5-11.9 | 11.70 | 0.20 | 1.7 |
| M <sub>3</sub>  | Length | 3 | 0 | 14.2-14.5 | 14.37 | 0.16 | 1.1 |
|                 | Width  | 2 | 0 | 12.5-12.7 | 12.60 | 0.14 | 1.1 |
| M <sub>4</sub>  | Length | 2 | 0 | 13.0-13.9 | 13.45 | 0.59 | 4.4 |
|                 | Width  | 2 | 0 | 11.7-12.5 | 12.10 | 0.57 | 4.7 |

\* All dimensions maximal, widths in molars across protoloph or protolophid, depth I<sub>1</sub> perpendicular to long axis of tooth.

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